

ODONATE PREDATION AS A FACTOR INFLUENCING DYTISCID BEETLE DISTRIBUTION AND COMMUNITY STRUCTURE

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ABSTRACT

Dragonfly larvae and predacious water beetles (Dytiscidae) are abundant predators in many shallow lentic habitats. The distributions of members of these two groups differ somewhat with odonates dominating in more open and permanent sites while dytiscids are more abundant in habitats of less stability and denser vegetation. It is postulated that predation of odonate larvae on dytiscids, especially the larval stages, is at least a contributory factor to this partitioning. Evidence in support of this hypothesis is drawn from general considerations of the biology and behaviour of the two groups, literature records, collecting experiences and a study that measured odonate density and the prevalence of dytiscids as food items in their guts. In certain Newfoundland bog pools, the density of odonate larvae is adequate to eliminate vulnerable dytiscids in a matter of days. Mechanisms by which dytiscids can avoid odonate predation are discussed.

INTRODUCTION

What governs the nature of natural communities? This question has generated much interest among biologists. The major conclusion to come out of the considerable research conducted on the question seems to be that there is no simple answer. Historical factors determine the suite of species present in a fauna that can interact potentially in communities. Abiotic tolerances determine which set of species can occur in a given physical arena. Within this arena, biotic interactions such as predation and competition further affect species densities and dispersion. Add to this niche and trophic specialization and temporal and behavioral similarities or differences among species, and the complexities of community organization are readily apparent.

Water beetle workers have recognized characteristic associations of water beetles species, at least within regional faunas. There is a long history of these associations being described and related to habitat characteristics. Recently, several authors (e.g. Larson 1985, Ranta 1985, Flechtner 1986, and Cuppen 1986) have used numerical techniques to define communities and relate species distributions to habitat parameters. Most studies of water beetle communities have emphasized the importance of physical, chemical and vegetal features of habitats as determiners of beetle distribution, although some authors have considered also predation and competition effects (Nilsson 1986, 1988).

There are two aspects to the problem of whether predation pressures have had a role in shaping dytiscid communities. First, past predation pressures may have been responsible for shaping aspects of the ecology, behaviour and morphology of

dytiscids, for example the development of defensive glands that produce a complex array of defensive substances (Dettner 1985), or the evolution of protective coloration by species in certain types of habitat (Young 1960). However, if these traits have become fixed because of this pressure, no direct evidence is left with which to demonstrate the relationship so that selection pressures for the evolution of the feature must be inferred based on concepts of its function. The second aspect involves current and continuing interactions where predation effects and outcomes are not stabilized and vary depending upon the conditions under which they occur. These sorts of interactions are amenable to observation and this aspect of predation interaction is considered here.

It is necessary, first, to establish if predators in aquatic systems are capable of exerting enough pressure on prey populations to modify the prey species mix, population structure, and/or their morphological traits. There is abundant evidence to indicate that many littoral habitats are predator dominated systems. When present, fish generally have a major impact on invertebrate communities, occupying the role of top predator by virtue of their large size and activity (Gilinsky 1984). Fish predation on invertebrates may result in elimination of species from a system, change the population densities, or change the morphology and behaviour of prey (Stenson 1978, Nilsson 1981, Morin 1984). Wilson (1923) was concerned about the impact of water beetle predation on fish in fish-culture ponds. However, he came to the conclusion that beetle larvae and adults are eaten freely by many fish, and that all beetle larvae and adults of smaller species constitute a very important item of fish food. Wilson reviewed and supported the observation made by many authors that dytiscids tend to be much less abundant and diverse in large ponds and lakes than in smaller bodies of water. With qualification, this observation is still generally valid (Larson 1985, Ranta 1985). It is probable that fish predation in larger bodies of water has a bearing on this distribution.

While fish are undisputably important predators, certain factors limit their distribution, *e.g.*, drying of habitat, oxygen depletion, freezing, and dense debris or plant structure in the habitat. Fish are absent from many northern lentic habitats. In such habitats, can other groups of predators exert the same type of impact on invertebrate communities on which they prey? If so, which groups of predators are likely to do this? Within the Insecta, Odonata, Hemiptera (which will not be considered here) and Coleoptera are especially diverse and abundant predators in lentic habitats. The relative abundance and success of each group varies from site to site. The purpose of this paper is to evaluate the evidence for predation by odonate larvae as a factor affecting the distribution of dytiscid beetles.

ODONATES AS SIGNIFICANT PREDATORS OF DYTISCIDS?

Evidence from literature and observation

Wissinger (1988) found large odonates increased in numbers to become top predators in the absence of fish. Benke (1976) recorded dragonfly larvae in very high densities in a South Carolina pond, where he concluded they were capable of rapidly annihilating their prey (most animals of suitable size [Pritchard 1964]) which survived only because they found refuges. The high density of odonate larvae observed by Benke is not unusual: for example Ball and Hayne (1952), Beatty and Hooper (1958) and Macan (1964) reported high densities of odonate larvae in shallow lentic habitats. In fact, the standing crop of odonates commonly may exceed that of their prey (Benke 1976). Thorp and Cothran (1984) showed that dragonfly predation can influence significantly a benthic community, primarily by changing prey density rather than community diversity. Density dependent

Table 1. Comparison of predation strategies of odonate and dytiscid larvae

	ODONATA	DYTISCIDAE
a	ambush and searchers hidden or not exposed deriving protection from predators	hunters, searchers exposed and mobile, at risk to predators
b	high assimilation rate of ingested food efficient predators	? probably less efficient predators
c	variable growth rate population taking wide range of prey sizes at any one time	less variation, population in synchrony in growth
d	ultimate size of larvae larger on average, growth slower	smaller larvae but growth faster

effects may be major factors controlling odonate communities (*e.g.*, Johnson *et al.*, 1985) and may result in both inter- and intraspecific asynchrony in growth so that odonates of a range of sizes are present to crop prey of a range of sizes.

Larson and Colbo (1983) suggested that odonates are significant predators of dytiscids. This idea derives from consideration of population densities, feeding methods and life history patterns of both groups. The most important interactions are probably between the larval stages because this is the only active stage of odonates to be in the water. Adult beetles appear to be fairly well protected from predation by size, hard cuticle and perhaps defensive secretions; larvae are apparently more vulnerable (Pritchard 1964, Griffiths 1973). Table 1 summarizes major differences in the predation strategies of odonate and dytiscid larvae.

Several lines of observation lend support to the idea that odonates negatively affect dytiscids. A few examples will illustrate this.

A. Numerous authors made the general observation that dytiscids are scarce in large lakes and are most numerous with the greatest diversity in seasonal habitats, newly formed ponds and the flooded margins or zone of dense emergent vegetation of larger ponds (Galewski 1971, Nilsson 1984, Larson 1985). Stability does not seem to favour many species. On the other hand, dragonfly larvae are generally not numerous or diverse in highly variable habitats, possibly due to their inability to cope with habitat drying (Fischer 1961) or freezing. In other words, there is somewhat of a habitat segregation between odonates and dytiscids. Historical and physical characteristics may limit the range of habitats occupied by odonates, but why are dytiscids not more successful in the habitat types occupied by odonates?

B. In 1986, John Carr and I sampled a series of small moraine ponds on the western slope of the Nahanni Mountains, Yukon Territories, along the Cantung

Table 2. Frequencies of co-occurrence of major taxa in habitats from which dytiscid beetles have been collected (after Flechtner 1986, Fig. 5).

Taxon	Frequency of co-occurrence (%)
Pisces	31
Odonata	39
Amphibia and Reptilia	40
Megaloptera (larvae)	40
Haliplidae	42
Heteroptera	44
Ephemeroptera and Plecoptera	51
Hydraenidae	52
Hydrophilidae	63
Trichoptera (larvae)	64
Diptera (larvae)	94

Road. The ponds ranged in elevation from the coniferous forest zone, through birch-lichen habitat to alpine habitats. Ponds within and near the coniferous forest zone had abundant odonates but few beetles which were largely confined to emergent vegetation at the very edges. Higher elevation ponds were superficially similar to those of lower elevations but odonate density was dramatically less while beetles were much more numerous. These ponds reflect a common faunal pattern for in general, with increasing elevation or latitude (at the highest latitudes), and deteriorating climates, beetles tend to be found more widely distributed in lentic habitats and occupy more open waters. For example, in barren alpine or arctic pools agabines and hydroporines occupy a wider range of depths and habitat types than is generally observed for lower elevation or lower latitude populations. Odonates are usually absent or in very low densities in such pools.

C. Some types of dytiscids occur regularly in habitats with dense populations of odonate larvae. These include: species of *Dytiscus* and *Cybister* which, because of their very large size, probably enjoy a switch in predator advantage; thermonectines, the larvae of which are pelagic and occupy a different zone than the dragonfly larvae; and very small species of dytiscids (e.g., bidessines) which generally occur among very dense detritus, in moss or algal mats, or in very shallow water right at the water's edge - zones in which odonate populations are low. Larson (1985) pointed out that the size distribution profile within the dytiscid

faunas of Alberta and Florida differed, with very small species comprising a proportionally much larger element in the Florida fauna. A partial explanation could be that the rich odonate (as well as fish) fauna of Florida selects for dytiscid forms that escape predation through adaptation to microhabitats which provide refuge from predators.

D. Flechtner (1986) challenged the suggestion of Larson and Colbo (1983) of a negative correlation between dytiscids and odonates. However, the data of Flechtner's Fig. 5 (reproduced in Table 2) which give percentage occurrence of various major taxa in collections with dytiscids, provide support for Larson and Colbo. It is significant that fish have the lowest co-occurrence (ca 30%) with dytiscids, followed by odonates (ca 38%). These data do not indicate how many samples contained either fish or odonates but not dytiscids, which would even further lower the co-occurrence rates.

Dytiscid beetles and larvae are subject to different predation pressures, with the larvae more vulnerable to predators. Life history theory predicts that selection acts to reduce the duration of the stage with the higher mortality rate (Wilbur 1980). This appears applicable to dytiscids, for in general, the larval stage is relatively short compared with the life span of adults. For example, even for the many species the life histories of which are not known, adults can be collected throughout much of the year while larvae appear to occur for a shorter and more specific period. This pattern of life history probably has more to do with habitat seasonality than predation (Larson 1985), but also could be reinforced by predation pressures.

A QUANTITATIVE ESTIMATE OF PREDATION

Diverse groups of insects, such as dytiscids and odonates, can be expected to interact in a variety of ways depending upon the taxa and habitats involved. A recent study on insect communities in a series of ombrotrophic bog pools (Larson and House 1990) provided an opportunity for a quantitative assessment of odonate predation on dytiscids in this habitat. The primary objective of the study was to determine abundance and distribution patterns of macroscopic animals within the pool system, and to interpret these in relation to habitat features and interaction patterns between taxa. For the purposes of this discussion, only the patterns observed for odonates and dytiscids will be discussed. Full details of the habitat and arthropod community structure are published elsewhere (Larson & House 1990).

The study was carried out on an ombrotrophic, domed bog located on the Avalon Peninsula 20 km south of St. John's, Newfoundland. The bog was treeless with the principal vegetation being sphagnum mosses, ericaceous shrubs, rushes and sedges. The bog contained in excess of 200 pools ranging in surface area from less than one to greater than 500 m². The pools were divided into four size classes based on their surface area, namely: Class A - > 100 m²; B - 10 to 100 m²; C - 1 to 10 m²; and D < 1 m²). In spite of the size differences, the pools were similar in water quality and form. Pool depth was positively correlated with surface area. Water level fluctuation was similar across all pools which meant that some of the smaller, shallower pools lost visible water during dry periods.

Pools were sampled by collecting all insects within a quadrat of 1 m². The entire area of pools less than 1 m² was sampled and the resulting counts transformed to numbers per m². Regardless of pool size, one edge of the quadrat was always formed by the pool bank so that edge effects were standardized across

Table 3. List of taxa collected and their density (number m^{-2}), (standard error) and prevalence (%) in pools of the four size classes. The numbers for Dytiscidae include pooled larvae and adults. * - mean density less than $0.1 m^{-2}$.

	POOL SIZE CLASS			
	D	C	B	A
surface area, m^2	< 1	1 - 10	10 - 100	> 100
# samples	14	28	54	13
ODONATA				
Coenagrionidae				
<i>Enallagma</i>	*	*	24.3 (5.6)	86.1 (25.0)
<i>cyathigerum</i> (Ch.)	7	4	89	100
Lestidae				
<i>Lestes</i>	0	*	1.3 (0.5)	1.0 (0.6)
<i>disjunctus</i> Selys	0	4	29	23
Aeshnidae				
<i>Aeshna</i>	0	0	5.0 (1.1)	1.7 (0.5)
<i>eremita</i> Scudder	0	0	77	69
<i>A. juncea</i> L.	0	*	*	0
	0	4	2	0
<i>A. sitchensis</i>	2.9 (1.2)	2.1 (0.5)	*	*
Hagen	57	56	4	8
<i>A. subarctica</i>	0	0.2 (0.1)	1.9 (0.5)	2.3 (1.0)
Walker	0	15	68	77
<i>A. umbrosa</i>	0	*	*	0
Walker	0	4	4	0
Corduliidae				
<i>Cordulia</i>	0	0.2 (0.1)	11.2 (2.0)	11.4 (3.9)
<i>shurtleffi</i>				
Scudder	0	11	84	84
<i>Somatochlora</i>	0	0	0.2 (0.1)	0.2 (0.1)
<i>cingulata</i> (Selys)	0	0	14	15
<i>S. forcipata</i>	0	*	0	0
Scudder	0	4	0	0
<i>S. septentrionalis</i>	0.1 (0.1)	0.5 (0.2)	8.8 (2.0)	4.8 (1.8)
Hagen	7	26	77	77
Libellulidae				
<i>Leucorrhinia</i>	1.9 (1.4)	8.9 (3.0)	38.9 (7.3)	13.6 (4.2)
<i>hudsonica</i> Selys	29	37	100	92
<i>Libellula</i>	6.6 (4.4)	7.0 (1.7)	0.5 (0.2)	0.5 (0.4)
<i>quadri-</i>				
<i>maculata</i> L	43	63	25	15
Total Odonata	11.5 (6.1)	19.2 (3.8)	92.2 (11.6)	121.7 (30.2)

(continued on next page)

Table 3 (continued)

	POOL SIZE CLASS			
	D	C	B	A
COLEOPTERA				
Dytiscidae				
<i>Acilius</i>	0	*	*	0
<i>semisulcatus</i> Aube	0	4	2	0
<i>Agabus</i>	0	0.1 (0.1)	0.1 (0.1)	0
<i>anthracinus</i> Mann	0	4	5	0
<i>A. confinis</i>	0.2 (0.1)	0	0	0
Gyllenhal	15	0	0	0
<i>A. inscriptus</i>	1.6 (0.7)	0.8 (0.4)	0	0
Crotch	46	7	0	0
<i>A. leptapsis</i>	0.7 (0.4)	0	0	0
LeConte	14	0	0	0
<i>Dytiscus</i>	0	0	*	0.2 (0.2)
<i>alaskanus</i> B.-B.	0	0	2	15
<i>Graphoderus</i>	0	0	0	*
<i>liberus</i> Say	0	0	0	8
<i>G. perplexus</i>	0	0	0.2 (0.1)	0.6 (0.5)
Sharp	0	0	13	23
<i>Hydroporus</i>	1.0 (0.6)	5.2 (4.0)	0.1 (0.1)	0.1 (0.1)
<i>badiellus</i> Fall	31	25	7	8
<i>H. brevicornis</i>	4.4 (2.3)	2.1 (0.9)	0	0
Fall	50	33	0	0
<i>H. morio</i>	1.2 (0.6)	0	0	0
Aubé	21	0	0	0
<i>H. notabilis</i>	0.1 (0.1)	0	0	0
LeConte	7	0	0	0
<i>H. obscurus</i>	8.2 (2.1)	4.3 (1.5)	0.4 (0.2)	0.1 (0.1)
Schaum	79	52	21	15
<i>H. paugus</i>	1.8 (0.6)	0.3 (0.1)	0	0
Fall	57	22	0	0
<i>H. rectus</i>	0.1 (0.1)	0	0	0
Fall	7	0	0	0
<i>H. signatus</i>	3.5 (2.2)	2.6 (1.2)	0	0
Mannerheim	21	33	0	0
<i>H. tristis</i>	0.5 (0.3)	1.5 (0.6)	0	0
Paykull	14	37	0	0
<i>Ilybius discedens</i>	1.7 (0.5)	1.1 (0.4)	*	0.1 (0.1)
Sharp	57	37	4	15
<i>I. pleuriticus</i>	0	0	3.7 (0.6)	0.5 (0.3)
LeConte	0	0	64	23
<i>Rhantus</i>	0.1 (0.1)	0	0	0
<i>binotatus</i> Say	7	0	0	0
<i>R. wallisi</i>	0.1 (0.1)	0.4 (0.1)	0.2 (0.1)	0.9 (0.5)
Hatch	7	33	13	46
Total Dytiscidae	25.2 (4.6)	18.4 (5.9)	4.7 (0.6)	2.5 (0.9)

Table 4. Odonate density and predation rates on dytiscids in bog pools

	POOL SIZE, M ²			
	<1	1 - 10	10-100	> 100
A. Odonate population density	11.5	19.2	92.2	121.7
B. Odonate predation rate (density (A) X prevalence of dytiscids in gut) dytiscids consumed/day/m ²	0.59	0.54	1.99	4.11
C. Beetle density	32.8	23.8	5.1	3.3
D. Prey clearance rate (days) C/B	55.5	44.1	2.5	0.8

samples. Sampling was conducted by repeatedly sweeping the quadrat with an aquatic net of 1 mm mesh, then visually picking insects from the sweepings. A quadrat was repeatedly swept until no further specimens were found.

A list of the species of Odonata and Dytiscidae and the density of each in pools of the four size classes is presented in Table 3. Beetle and odonate densities (logten (number m⁻²+1)) were inversely correlated ($r = -0.39$, $p < .01$). Beetle populations were densest in the smallest pools and decreased rapidly with increasing pool size, while odonate populations were more than ten times as dense in the A pools as in the D pools.

Size of adult beetles was positively correlated to pool size ($r = 0.56$, $p < .01$). The correlation was calculated between mean adult size of each species represented in each pool and pool surface area. Thus, the occurrence of a species in a pool was treated as a single observation. If the size of each individual and the pool size in which it was found were correlated, the relationship would be even stronger. Generally, small species occurred in small pools: however, *Hydroporus badiellus* Fall and *H. obscurus* Schaum also occurred in low frequencies in the A and B pools. This was a result of including a length of bank in each sample, because these species occur in the moss at the water's edge. If the samples were taken farther from the bank so as to exclude these peripheral species, the pool size - beetle size correlation would strengthen.

To determine if the odonates actually were preying upon dytiscids, gut contents of 500 odonate larvae, representing the five most abundant species collected from pools of all sizes from May through October, were examined. Some specimens of all species were found with dytiscid larvae in their guts and the *Aeshna* species also contained hydrophilid and hydroporine adults. Prevalence of dytiscid remains in the gut contents of these species ranged from 0.7 % in *Leucorrhinia hudsonica* Selys to 15% in *Aeshna sitchensis* Hagen. If prevalence of

dytiscid remains in the gut of each species of dragonfly is multiplied by the density of the respective species in pools of each size class and these values then summed, an estimate of the predation rate of dragonflies on dytiscids can be obtained (Table 4). If it is assumed that residence time of material in a dragonfly gut is one day (indicated by Pritchard 1964) then this figure represents the daily predation rate of dragonflies on dytiscids averaged over the ice-free season - the period over which odonate larvae were collected for gut content analysis. Dividing the mean density of dytiscids by this predation rate gives an estimate of the length of time it would take for odonates to eliminate the dytiscid population from each habitat type (Prey clearance rate, Table 4). This is highly simplified with many possible sources of error such as the fact that "dytiscids" includes both adults and larvae and that adults may not in fact be at risk to predation. Nevertheless, the figures still indicate that odonates exert a powerful predation pressure on dytiscids and that in the presence of a dense odonate population, low dytiscid numbers may be explained by predation.

In this study, the most abundant dytiscid in the larger pools was *Ilybius pleuriticus* LeConte (Table 3). This is the largest North American *Ilybius* (Larson 1987), and occurs in deeper and more open water habitats than other members of the genus. Its larvae crawl around on the substrates, generally in habitats with dense odonate populations. Why are they not annihilated by dragonflies? *I. pleuriticus* larvae are distinctive among known North American *Ilybius* larvae (unpublished data) in that they have a very bold pattern of longitudinal stripes extended the length of the dorsal surface of the body. Perhaps this striped pattern makes the larvae more difficult for an odonate larva to hit with a visually aimed labial strike. By itself, this explanation is not compelling. However, within the same habitat are two species of *Aeshna*, *A. eremita* Scudder and *A. subarctica* Walker. *Aeshna* larvae probably behave more like dytiscid larvae than do other dragonfly larvae, *i.e.* they are rather active and move around considerably. As cannibalism occurs amongst odonate larvae, the small *Aeshna* larvae should be at risk to odonate predators due to their movement. Larvae of both *Aeshna* species are very boldly coloured: *A. eremita* larvae are black with the middle third of the body pale yellow; *A. subarctica* larvae are longitudinally striped, similar to that of larval *I. pleuriticus*. The color pattern of both *Aeshna* species is very disruptive to the human eye. These markings are strongest on the smallest larvae, tending to obliterate in larvae of 10 to 15 mm length, with the larger specimens more uniformly dark.

The most probable function of color pattern is to provide protection from visually hunting predators. If the predators were vertebrates, it would seem most likely that the predation pressure would become more intense as larvae became larger thus large larvae should possess protective coloration. But it is the small larvae that have the disruptive color pattern and this pattern disappears at about the size that larvae become large enough to escape odonate predation. Thus it is probable that strikingly disruptive color patterns are a defense against odonate predation.

EXPERIMENTS AND CAVEATS

If dragonflies are important predators on dytiscids, removal of odonates from a habitat should result in an increase in beetle density and also perhaps in a broadening of range of habitat occupied by at least the larvae. Such an experiment has not been conducted specifically to test the impact of odonates on beetles. However, Benke (1978) did a removal experiment in which odonate populations

were reduced within pond enclosures and he noted an increase in prey abundance and survivorship of remaining odonates.

Laboratory rearing confirms the finding from gut content analysis: odonates prey on smaller dytiscid larvae and strike at adults although they may have difficulty in handling them (Pritchard 1964, Griffiths 1973). However, laboratory studies should be done to determine patterns of interaction occurring across a range of sizes of dytiscids and odonate larvae. Is there a size of dytiscid adult or larvae which is too large or active for particular odonate species to capture or handle? Are the tables turned by large dytiscids? Large larvae of species of *Dytiscus* and *Cybister* can prey upon large odonate larvae. For example, third instar larvae of *D. alaskanus* Balfour-Browne successfully attacked *Aeshna* larvae that had been thrown back into a pond after being collected in a dip net (B.C., Cassiar Road km 723, July 18, 1987). R. Trottier (pers. comm., 1987), studying the large odonatid, *Anax junius* Drury, in southern Ontario thought that *Dytiscus* larvae were preying upon the dragonfly larvae. Compared to dytiscids, odonates hatch at a small size and grow slowly through a large number of instars. Probably these small odonates are suitable prey for many dytiscids.

The extent of dytiscid larval predation on odonates will be difficult to determine. Because dytiscid larvae feed on prey fluids, predation could be determined only through direct observation or by serological analysis of gut contents. In any event, high predation rates on odonate larvae may not have a major effect on trophic patterns. There is evidence that many habitats are overstocked with dragonfly larvae such that cannibalism and competition are severe and limiting. In such situations, mutual predation between dytiscids and odonates probably would favour the odonates for the lower starting populations of dytiscids put them at a disadvantage. Based on consideration of predation characteristics (Table 1), it is predicted that under conditions of low prey density odonates will out-compete dytiscids. This could be tested in the lab.

Although it has not been proven that odonate larvae have a major impact on dytiscid distribution and abundance, there is much evidence to suggest this is so. Odonate predation must be less important than physical suitability and trophic opportunities as factors structuring lentic dytiscid communities. However, predation and competition pressures within shallow lentic habitats are significant factors shaping resident communities and dytiscids can not be immune to these forces. Many of their behaviours and adaptations are likely to be responses to such biotic pressures.

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